

A TENTATIVE ANALYSIS OF THE SPIDER FAUNA OF SOME TROPICAL OCEANIC ISLANDS

L. BAERT AND R. JOCQUÉ

Baert, L. and Jocqué, R. 1993 11 11: A tentative analysis of the spider fauna of some tropical oceanic islands. *Memoirs of the Queensland Museum* 33(2): 447-454. Brisbane. ISSN 0079-8835.

The spider fauna of oceanic islands in the Pacific (Galápagos, Juan Fernandez, Easter Island, Marquesas, Hawaii), the Atlantic (Saint Helena) and the Indian Ocean (Comoros, Seychelles) is analysed. Family composition, size frequency distribution, species/area relationship, the origin of the faunas and their qualitative compositions are discussed. The colonization of the islands by spiders appears to be greatly influenced by the accessibility of the island, its habitat diversity and the speciation capacity of particular groups. Most of the fauna is composed of species transported by man. Thorough analysis of island faunas is still hampered by the lack of complete published data sets.

Les faunes aranéologiques des îles océaniques situées dans le Pacifique (Galápagos, Juan Fernandez, Marquises, Hawaii) l'Atlantique (Sainte-Hélène) et l'Océan Indien (Comores, Seychelles) sont analysées. Leur composition au niveau de la famille, la distribution des fréquences de taille, leur origine et leur composition qualitative sont discutées. La colonisation des îles par les araignées semble être fortement influencée par l'accessibilité de ces îles, leur diversité en habitats et la capacité de spéciation de certains groupes. Une grande partie des faunes est composée d'espèces apportées par l'homme. Une analyse complète des îles océaniques est encore impossible à cause du manque de données complètes publiées.
□ *Araneae, island zoogeography.*

Leon Baert, Koninklijk Belgisch Instituut voor Natuurwetenschappen, Vautierstraat 29, B-1040 Brussels, Belgium; Rudy Jocqué, Koninklijk Museum voor Midden-Afrika, B-3080 Tervuren, Belgium; 26 October, 1992.

Most studies of island spiders have been confined to the description and enumeration of species. A general explanation of the composition of the araneological fauna of islands has not been tried. The availability of many almost complete species lists of remote oceanic and granitic islands allows us to analyse these spider faunas and try to understand their compositions. Only a few data-sets (those of Galápagos and Saint Helena) are nearly complete and most others are likely to grow considerably. For several islands the species lists included many unidentified species submitted for study to us or present in other collections (e.g. Cocos: Natural History Museum of Los Angeles County). Nevertheless we have tried to find patterns in the composition of the tropical island spider faunas.

MATERIAL AND METHODS

Apart from the spiders of the Galápagos and the Comoros, all data used are from the literature (Table 1). Hence, in the analysis of the size distribution, we had to use the total length, which is a less reliable measure than carapace width or the size of another sclerotised body part.

To compare the family composition, the num-

ber of species in each family was expressed as a percentage of the total number of species. The Renkonen-index was used to calculate the percentage of similarity.

RESULTS AND DISCUSSION

FAMILY SIMILARITY

Because the islands are in different zoogeographical provinces, a comparison of their faunas on the species level is not informative.

Similarity on family level was surprisingly high between the Galápagos, the Hawaiian Archipelago (Pacific) and Saint Helena (Atlantic), reaching ca 70% (Fig. 1). A second group (ca 60% similarity) consists of the Seychelles and Cocos Islands. These distinct vegetation belts, as on the main islands of the first group, seem important and induces a similar family composition. These islands were initially covered entirely by forest. The southern pacific Easter Island and Juan Fernandez, now covered by a gramineous, so called pampa-vegetation, have little similarity in family constitution.

BODY LENGTH FREQUENCY DISTRIBUTION

In tropical continental habitats, e.g. savanna

Island/archipelago	Area _i (km ²)	Highest elevation (m)	Distance to nearest continent (km)	Age (my)	Literature Consulted
Cocos I. (CO)	46.6	849	500 (Costa Rica)		Hogue and Miller (1981)
St Helena I. (SH)	120	705	1800 (Africa)	14.3	Benoit (1977)
Easter I. (PA)	165.8	530	3760 (Chile)	2.5	Skottsberg (1920), Berland (1924)
Juan Fernandez I. (JF)	178	1500	660 (Chile)	10	Skottsberg (1954)
Seychelles Arch. (SE)	273	914	932 (Madagascar)	65	Benoit (1978a, b), Saaristo (1978)
Marquesas Arch. (MA)	1274	1200	6300 (Peru)		Berland (1935, 1939)
Galápagos Arch. (GA)	7882	1707	960 (Ecuador)	9	Jackson (1985), Baen <i>et al.</i> (1989a, b)
Hawaii Arch. (HA)	16504	4206	4000 (Mexico)	70	Suman (1964, 1965), Gertsch (1973)
Comoros Arch.	2237	2300	300 (Madagascar)	1	Jocqué (1985)

TABLE 1
Summary data (age is approximate) of islands and archipelagos considered.

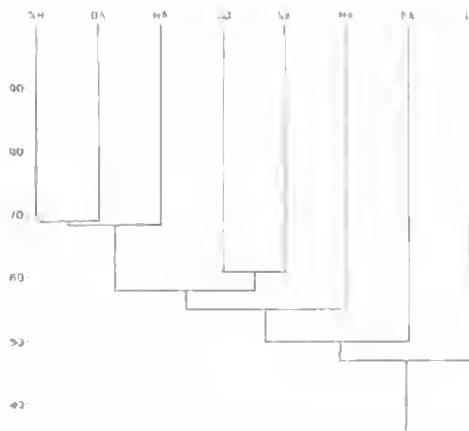


FIG. 1 Dendrogram of the similarities between the islands/archipelagos on family level.

and secondary forest in Ivory coast (Jocqué, 1980), middle-size spiders in the class of 4-6mm dominate (Fig. 2). However, data for Ivory Coast are based entirely on pitfall trap samples. That may bias the size frequency distribution towards higher or lower averages. On the other hand, the collections from islands are clearly biased towards larger spiders. Earlier collectors are more likely to have taken conspicuous large webspiders than small soil dwelling spiders. As for the other analyses it is probably too early to detect relevant differences in size distributions on different islands as compared to the situation on the continent.

Only spiders from Galápagos, Cocos Island and

TABLE 2. Mean body length (mm), number of species and standard deviation (RCI = Ivory Coast).

	SH	SE	PA	CO	GA	JF	MA	HA	RCI
\bar{x}	6.75	5.57	6.45	4.79	5.52	7.63	6.40	6.82	5.82
n	95	125	22	29	136	31	41	127	134
SD	4.47	4.62	3.47	4.20	4.23	5.58	3.35	3.98	3.91

the Seychelles seem on average smaller than those from the collections made with pitfall traps in West Africa (Table 2). As only the difference GA-RCI is significant ($\chi^2 = 23.84$; $P < 0.02$) it seems that the discrepancies are further meaningless. However, complete data from the islands and fully comparable data from the continent might reveal more differences in average size of island and continental spiders. We expect selection to favour small spiders during the colonisation process. Thus, many more small spider species are likely to be present on islands than on the continent. Smaller spiders live in higher densities than bigger ones and the possibility that they reach an island is statistically higher than for larger spiders. Moreover, smaller spiders are usually better aeronauts although young stages of larger spiders have often been observed to balloon as well. The chance that a raft-rafting being an important mean of colonisation—contains a 'propagule' is also likely to be higher for smaller spiders than for larger ones.

However, the possibility for survival of spiders that reach an island is probably better for larger than for smaller ones but the enormous differences in specific ecophysiological characters make it difficult to generalise.

The Seychelles are granitic continental fragments and must have had a well-balanced fauna when they separated from the mainland. Hence, they should have elements of a continental spider fauna. Apparently this is not so. Some unusually large soil-dwelling spiders do exist on the island (see below), but the smallest size class seem more important on that archipelago, just as on the others. The Seychelles are a group of small islands with the largest not exceeding 15km². When ocean levels were higher these islands must have been tiny and the chance for extinction very high. Larger spiders occur in smaller populations. Thus, they are more liable to become extinct hence the otherwise unexpected dominance

of smaller spiders on the Seychelles. The spider fauna of Seychelles is probably too little known because the two main expeditions (Benoit 1978, Saaristo 1978) were in the dry season.

Frequency distribution histograms for the smaller Pacific islands (Easter, Juan Fernandez and Cocos) and for the Marquesas archipelago, show very irregular shapes. The distribution seems to have several peaks.

There may be several reasons for this:

1 the fragmentary knowledge of their spider fauna. Few spider species are listed for these islands in the literature. Occasional samples, made by other zoologists during brief visits to Easter Island, yielded important new records of spider species. That is apparently true of our knowledge of the spider fauna of most tropical islands.

2 Cocos and Easter Island are still too young or are so isolated (Easter Island in the centre of the South Pacific Gyre; Juan Fernandez amidst the northerly directed Humboldt Current) that they are difficult to colonise and an equilibrium in their spider communities has not yet been reached.

3 due to their limited size and low habitat diversity these islands cannot support more species and do indeed have several size distribution peaks.

RELATION BETWEEN ISLAND AREA AND SPECIES DENSITY

Tropical African oceanic islands are far richer in species and their species/area relationship is much higher (0.48-0.81) than for tropical Pacific oceanic islands (Table 3). The very small Cocos Island lying the closest to a continental landmass is exceptional in this respect (0.60). Tropical Pacific archipelagos (0.01-0.04) and the southern Pacific islands (0.14-0.18) have relatively low species/area relationships. It is not clear why the African off-shore islands are so much richer than the others. The source areas may be richer but that must be proven by thorough studies of the continental spider faunas. Many more species may have been introduced on the African islands. This is probably true for Saint Helena that has an unusual large proportion (44%) of introduced spiders, mainly from temperate regions. It is doubtful whether that is a sufficient explanation.

There is a relationship between altitude (highest elevation) of the island and the number of species present (Fig. 3.1: $r = 0.677$, $p > 0.01$) and between area of the island and the number of

species present (Fig. 3.2: $r = 0.716$, $p > 0.001$). In both cases there is a significant correlation.

ORIGIN OF FAUNAS

As the distance from an island from the mainland increases, its component of continental species decreases.

Very striking is the much lower percentage of continental species on the African islands as compared to those of the Pacific. The same is true for the southern Pacific islands Juan Fernandez and Easter Island. This could be explained by their isolated position. Juan Fernandez lies in the middle of the northerly directed Humboldt Current, whereas Easter Island is situated a long distance from the continent in the centre of the South Pacific Gyre, making the arrival by rafting rather unlikely.

The presence on the Galápagos islands of northern, central (with Antillean elements), as well as southern American elements, could be explained by their special situation astride the equator. The archipelago lies in such a position that it is reached by the warm Niño Current in the rainy season and by the cold Humboldt Current in the dry season. The Californian Current of the Northern Hemisphere runs southwards along the North American coast and reaches the Panama Basin where it is warmed up and turns towards the Galápagos as the Niño Current. The southern Humboldt Current runs northwards along the south American coast and turns westward near the equator towards the Galápagos. Rafts can easily be transported from the north as well as from the south. A floating raft takes about two to four weeks to reach the islands from the South American mainland (Schatz, 1991).

Furthermore, there was a broad connection between the Caribbean region and the eastern Pacific area from 48 my until 3.5-3 my ago (Woodring, 1959; Jones and Hasson, 1965) with a sea current running from the Atlantic to the Pacific (Petuch, 1982). The Panama isthmus was plugged some 3 my ago by the Caribbean Plate which was shoved in between the north and south American plates. At that time the Galápagos islands had already emerged from the sea. It is acceptable that many fauna elements of the Caribbean reached the Galápagos at that time. Nearly 82% of the known spider species of Cocos Island are continental species.

The Marquesas have more species of Pacific origin. This can be expected because of the position of this archipelago at the margin of the Polynesian province (NE end of the south

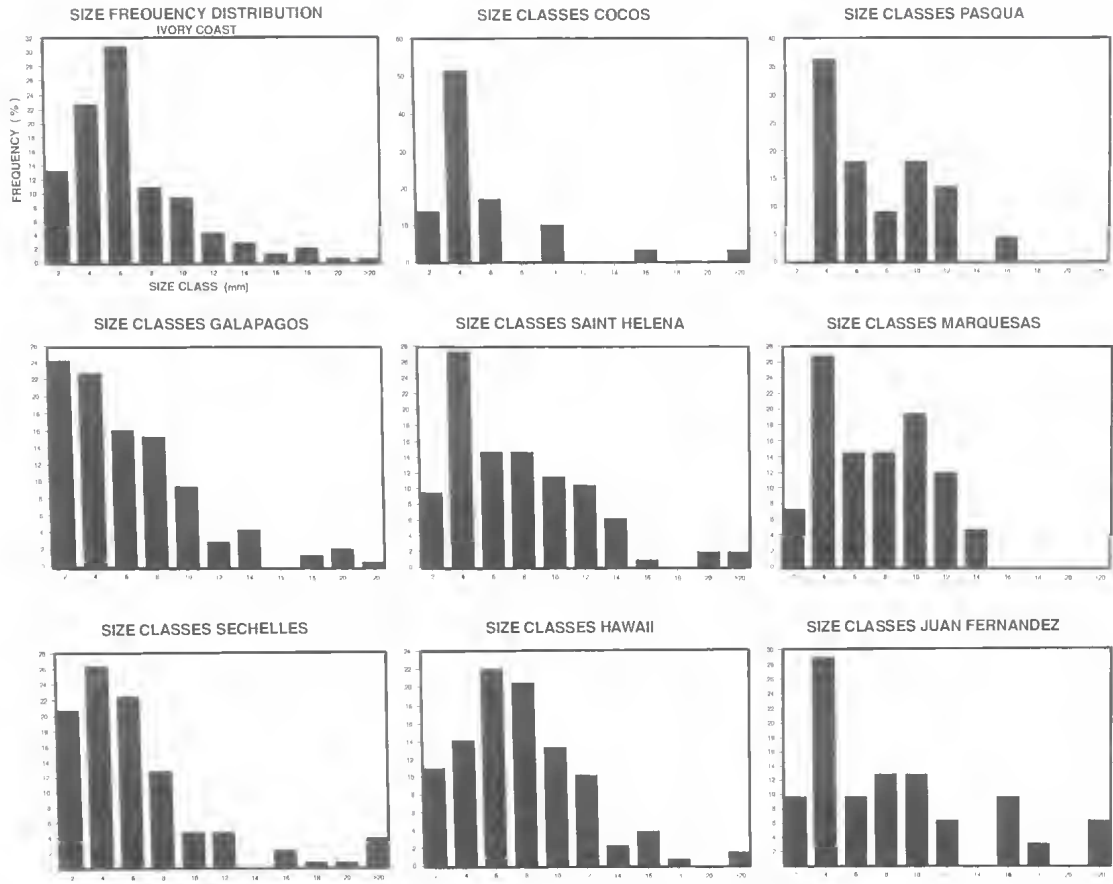


FIG. 2. Frequency distribution histograms of total body length (over 2mm size classes) for each island or archipelago.

equatorial archipelagos chain). In contrast, Hawaii and Galápagos have only a low percentage of Polynesian species as the distances between them and the Polynesian archipelagos are too extensive.

The term 'endemic' must be used now with great care because the continental faunas are far from being well known. This is especially so for the neotropical spider fauna. Many regions have

been sampled only superficially or not at all. Few families have been thoroughly revised and new studies will be needed once the 'black holes' have been filled. For instance, the figures in table 2 for Galápagos are based upon 70% of the total of the recognised species. Hence, 46 species have yet to be identified. At this stage in our knowledge one is never sure that the species one describes from an oceanic island really has a dispersion restricted

Island/Archipelago	S	S/area	Continental distribution	Pacific origin	Cosmopolitan species	Endemic
Cocos I. (CO)	30	0.63	82% (A)			18%
Galápagos Arch. (GA)	146	0.02	32% (A)	4%	9%	60%
Hawaii Arch. (HA)	168	0.01	11% (A)	5%	19%	64%
Marquesas Arch. (MA)	48	0.04		31%	20%	50%
Juan Fernandez I. (JF)	32	0.18	17% (A)		17%	70%
Easter I. (PA)	23	0.14	22% (AU)		66%	12%
Seychelles Arch. (SE)	131	0.48	9% (E)		18%	65%
St Helena I. (SH)	98	0.81	7% (E)	44%	45%	

TABLE 3. The spider fauna of islands and archipelagos. Percentage of species with distribution 1° continental (A=American; E=African; Au=Australian), 2° cosmopolitan and 3° species known only from island or 'Endemic'. Values based only on described species.

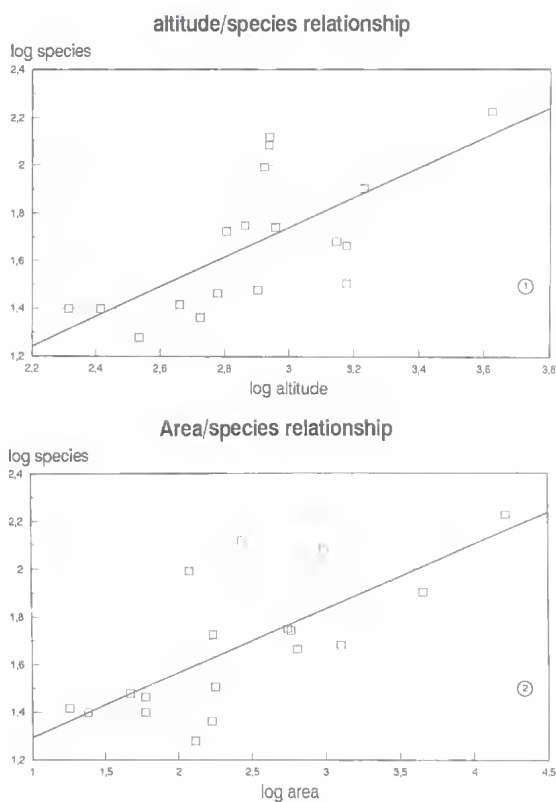


FIG. 3. 1, 2. Relationship between no. of spider species (N) and: 1, altitude (highest elevation) of island or archipelago ($\log N = -0.6224 \log \text{alt. (m)}$); 2., island/archipelago area ($\log N = 0.2686 \log \text{area} + 1.0269$).

to that island for it may not yet have been found on the continent. We may therefore seriously question whether we can validly use the proportion of endemics for the analysis of an island fauna. However, we consider that the percentage of endemics we now recognise reflects the rough proportion of real endemics that will eventually be shown to exist.

Cocos Island seems to have few (18%) 'endemic' species. It lies relatively close to the continent. Once the distance to the continent exceeds 900km, we find an 'endemic' proportion in between 50 and 65%. The high percentage of 'endemics' on Hawaii (64%) is probably due to its old age and thus the long period of isolation of the archipelago. The high percentage for the Galápagos islands (60%) may perhaps be due to the fragmentary knowledge of the South American spider fauna (the main reason why one third of the Galápagos spider fauna is not yet identified).

The high percentage (70%) of 'endemics' on

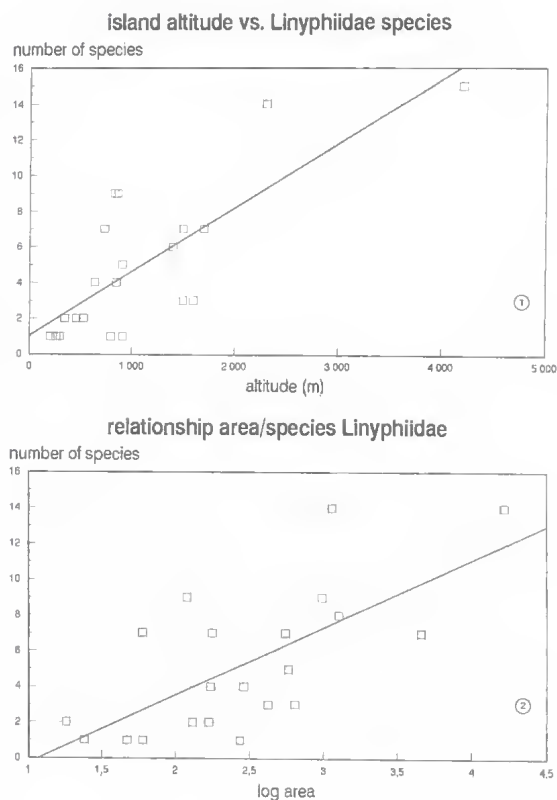


FIG. 4.1, 2. Relationship between no. of linyphiid species (L): 1, and altitude ($L = 0.0035 \text{ alt(m)} + 1.0544$; 2., and island/archipelago area ($L = 3.7886 \log \text{area} - 4.0344$) (separate islands in archipelagos). (S = no. species).

Juan Fernandez is very striking. Though close to the mainland, it is a rather isolated island (Humboldt Current) with an environment rendered harsh by the very special climatological conditions.

The proportion of cosmopolitan species on the islands varies between 0 and 20%, with two striking exceptions: Saint Helena with ca 44% and Easter Island with 60% (this figure is based on only 10 species). Most of these species are introduced and restricted to human settlements. This shows the great impact man has had on the spider fauna of Saint Helena.

All the islands considered here do have human settlements, native on Hawaii, Easter Island and Marquesas, but immigrated in historical times on the others. Human settlements invariably result in deforestation for arable land and subsequent introduction of ubiquitous species. Most often this is detrimental to the original fauna. Even more damage can be done with the introduction of

domesticated animals (cattle, dogs, cats, rodents, etc.) and cultivated plants. Accidental introductions can also have serious consequences as for instance the Little Fire Ant (*Wasmannia auropunctata*) on Galápagos. This species haunts large areas, devastating nearly all living animal organisms.

QUALITATIVE ANALYSIS

Qualitative analysis of the distribution of particular groups on islands is perhaps more revealing than quantitative analyses which are still hampered by the incompleteness of many data sets.

Spiders that do not balloon do not seem well adapted to colonise oceanic islands. Good examples are seen in the Zodariidae. Only four species, if we include *Cryptothele*, are present on the islands considered. On the Seychelles we find the endemic *Cryptothele alluaudi* Simon; the Comoros have *Asceua radiosa* Jocqué on Grande Comore and *Diores seluganus* Jocqué on Mohéli (Jocqué, 1986). *Zodarion trispinosum* Suman is known from Hawaii. The presence of a *Zodarion* on Hawaii, completely outside its main distribution is puzzling, but is probably explained by an introduction as is the presence of *Z. fulvonigrum* (Simon) in North America. The Mygalomorphae are found only on two of these archipelagos. Six species in three families (Benoit, 1978) occur on the Seychelles. Five of these are endemic, the sixth species, *Idiopsis intertidalis* (Legendre and Benoit), is also found on Madagascar and Grande Comore, where it occurs together with the endemic *Moggridgea nesioti* Griswold. The presence of these spiders, all but one apparently true endemics, on the Seychelles is explained by its granitic nature, which implies that they have had a fauna from the moment they were separated from the continent. The Comoros are probably more easily colonised than other islands, possibly by rafting, as that archipelago is close to its source area, Madagascar, for which the spider fauna is unfortunately poorly known.

Linyphiidae can be considered excellent colonisers mainly because many frequently balloon. However, linyphiids appear to be able to occupy few habitats. Jocqué (1984, 1985) explained that interference competition in tropical lowland with ants is apparently too important to allow the presence of many linyphiid species. As ants are less common at higher altitude many more linyphiid species tend to be present in highland than at low elevations (e.g. Scharff, 1992). (Since ant diversity and density are linked to

climatic conditions, the impression may exist that they are the determining factor.) The presence of an important number of Linyphiidae on high islands was already illustrated for the Comoros (Jocqué, 1985). This is particularly true for islands. There is a significant correlation between the altitude of island and the number of species of Linyphiidae present (Fig. 4.1: $r = 0.780$, $p < 0.001$) and between area of the island and the number of linyphiid species present (Fig. 4.2: $r = 0.688$, $p < 0.001$). There is a third aspect relevant to the colonisation of islands: parapatric speciation on the spot. The Lycosidae are a good example. Wolf spiders might be expected to be good colonisers. Their juvenile stages are active ballooners, and transport by rafting is also a likely means of dispersal if only because lycosids are very common on banks of rivers and in marshes from where rafts are supposed to be derived. However, the number of insular species is quite low compared to the high number of species in continental tropical areas. (Galápagos: 6 species; Hawaii: 11; Cocos: 1; Juan Fernandez: 2; Saint Helena: 7; Seychelles: 2; Comoros: 3). Moreover, almost all species from islands in this study have no continental distribution and must be considered endemics of each island. Only *Bristowiella seychellensis* (Bristowe) is known from both Seychelles and Comoros. Their apparently high speciation rate may be related to this. Of special note, some species at high altitudes on some islands are apparently derived from species at low altitudes. A well documented case is that of *Bristowiella* on the Comoros where two closely related species have clearly differentiated habitats: *Bristowiella seychellensis* living in short grassy vegetation from sea level to about 1500m and *Bristowiella kartalensis* Alderweireldt living in recent lava flows with sparse vegetation from about 600m upwards (Alderweireldt, 1988). Another interesting case is that of the Hawaiian cave dwelling lycosids which have strongly reduced eyes or none and which clearly speciated on the islands themselves (Gertsch, 1973).

On Galápagos, a group of six species apparently derived from the most common one ('Lyc 3'). It occurs over the whole archipelago and occurs mainly in coastal salt marshes. Another species ('Lyc 5') occurs only on the low island Española. The four other species are confined to the high pámpa zones of the volcanoes Sierra Negra and Cerro Azul ('Lyc 1') on Isabella, on San Cristóbal ('Lyc 2'), on Santa Cruz ('Lyc 4') and the Alcedo volcano on Isabella ('Lyc 6'). The revision of this remarkable species-group is in preparation.

A fourth example of such segregated parapatric populations is found on Juan Fernandez where 2 *Lycosa* species are found, one living along the coast, the other living in the higher pampa zone.

These statements reveal three important factors influencing the composition of island faunas. In the first place, there is the accessibility of the island, mainly its distance to a source area. In the second place, the diversity of the island's habitats is important. Particular spiders such as mygalomorphs and zodariids are only present on those islands that are easily reached or already had a fauna when they became isolated. Other families, although good colonisers, appear to be restricted by the ecological conditions of the island they can reach. Speciation appears to be the third factor which may be important in the colonisation of habitats that can hardly be reached by the normal ways of dispersal. The effect of niche pressure (Jocqué, 1982) is likely to be an important mechanism in this respect.

CONCLUSION

The faunal composition we now find on many islands is far from being natural. At the same time we know little about the arthropod fauna of most oceanic islands. This makes the analysis and comparison of the faunas very hard. The influence of speciation processes is probably largely overlooked in connection with the compensation of extinction.

LITERATURE CITED

- ALDERWEIRELDT, M. 1988. On the genus *Bristowiella*, with the description of *B. kartalensis* n. sp. from the Comoro Islands (Araneae, Lycosidae). *Bulletin of the British Arachnological Society* 7: 269-272.
- BAERT, L., MAELFAIT, J.-P. & DESENDER, K. 1989a. Results of the Belgian 1986 -expedition: Araneae, and provisional checklist of the spiders of the Galápagos archipelago. *Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen* 58: 29-54.
- 1989b. Results of the Belgian 1988-expedition to the Galápagos islands: Araneae. *Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen* 59: 5-22.
- BENOIT, P. 1977. Araneae. Introduction. In 'La Faune terrestre de l'île de Sainte-Hélène. Quatrième partie'. *Annales van het Koninklijk Museum voor Midden-Afrika, Zoologische Wetenschappen* 220: 12-188.
- 1978a. Contributions à l'étude de la faune terrestre des îles granitiques de l'archipel des Séchelles. Introduction. *Revue de Zoologie Africaine* 92: 390-404.
- 1978b. Contributions à l'étude de la faune terrestre des îles granitiques de l'archipel des Séchelles. Araneae Orthognatha. *Revue de Zoologie Africaine* 92: 405-420.
- BERLAND, L. 1924. Araignées de l'île de Pâques et des îles Juan Fernandez. In 'The Natural History of Juan Fernandez and Easter Island'. Vol. III, *Zoology*: 419-437.
1935. Araignées des îles Marquises. In 'Marquesan Insects-II'. *Bernice P. Bishop Museum Bulletin* 114: 39-70.
1939. Nouvelles araignées marquisiennes. In 'Marquesan Insects-III'. *Bernice P. Bishop Museum Bulletin* 142: 35-63.
- GERTSCH, W. 1973. The cavernicolous fauna of Hawaiian lava tubes. 3. Araneae (Spiders). *Pacific Insects* 15: 163-180.
- HOGUE, C. & MILLER, S. 1981. Entomofauna of Cocos Island, Costa Rica. *Atoll Research Bulletin* 250: 29pp.
- JACKSON, M. 1985. 'Galápagos, a natural history guide'. (The University of Calgary Press).
- JOCQUÉ, R. 1980. 'Verspreidings-, aktiviteits- en grocipatronen bij spinnen (Arancida), met speciale aandacht voor de arachnofauna van de Kalmthoutse heide'. (Doctoraatsverhandeling Rijksuniversiteit Gent). 181 pp.
1982. Niche pressure and the optimum exploitation hypothesis. *Biologisch Jaarboek Dodonaea* 50: 168-181.
1984. Considérations concernant l'abondance relative des araignées errantes et des araignées à toile vivant au niveau du sol. *Revue Arachnologique* 5: 193-204.
1985. Linyphiidac (Araneae) from the Comoro Islands. *Revue de Zoologie Africaine* 99: 197-230.
1986. Ant-eating spiders from the Comoros (Araneae, Zodariidae). *Revue de Zoologie Africaine* 100: 307-312.
- JONES, D.S. & HASSON, P.F. 1965. History and development of the marine invertebrate faunas separated by the central american isthmus. Pp. 325-356. In Stehli F.G. and Webb S.D. (eds). 'The Great American Biotic Interchange'.
- MACARTHUR R.H. & WILSON, E.O. 1967. 'The theory of island biogeography'. (Princeton University Press; new Jersey). 198pp.
- PETUCH, E.J. 1982. Paraprovincialism: remnants of palcoprovincial boundaries in recent marine molluscan provinces. *Proceedings of the Biological Society of Washington* 95: 774-780.
- SAARISTO, M. 1978. Spiders (Arachnida, Araneae) from the Seychelle Islands, with notes on taxonomy. *Annales Zoologici Fennici* 15: 99-126.
- SCHARFF, N. 1992. The Linyphiid fauna of Eastern Africa (Araneae, Linyphiidae). Distribution, patterns, diversity and endemism. *Biological Journal of the Linnean Society* 45: 117-154.
- SCHATZ, H. 1991. Arrival and establishment of Acari

- on oceanic islands. Pp. 613-618. In Dusbábek F. and Bukva, V. (eds). 'Modern Acarology'. Vol. 2. (Academia, Prague and SPB Academic Publishing: The Hague).
- SKOTTSSBERG, C. 1920. Notes on a visit to Easter Island. Pp. 2-20. In 'The Natural History of Juan Fernandez and Easter Island'. Vol. 1.
1954. A geographical sketch of the Juan Fernandez Islands. Pp. 89-192. In 'The Natural History of Juan Fernandez and Easter Island'. Vol. 1.
- SUMAN, T. 1964. Spiders of the Hawaiian Islands: Catalog and Bibliography. *Pacific Insects* 6: 665-687.
1965. Spiders of the Family Oonopidae in Hawaii. *Pacific Insects* 7: 225-242.
- WOODRING, W.P. 1959. Geology and paleontology of canal Zone and adjoining parts of Panama. Description of Tertiary mollusks (Gastropoda: Vermetidae to Thaididae). United States Geological Survey Professional Paper 306: 147-240.